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Population level interactions between an invasive woodwasp, an invasive nematode and a community of native parasitoids

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Abstract

Parasitic nematodes and hymenopteran parasitoids have been introduced and used extensively to control invasive Eurasian *Sirex noctilio* woodwasps in pine plantations in the Southern Hemisphere where no members of this community are native. *Sirex noctilio* has more recently invaded North America where *Sirex*-associated communities are native. *Sirex noctilio* and its parasitic nematode, *Deladenus siricidicola*, plus six native hymenopteran woodwasp parasitoids in New York and Pennsylvania, were sampled from 204 pines in 2011–2019. *Sirex noctilio* had become the most common woodwasp in this region and the native parasitoids associated with the native woodwasps had expanded their host ranges to use this invader. We investigated the distributions of these species among occupied trees and the interactions between *S. noctilio* and natural enemies as well as among the natural enemies. *Sirex noctilio* were strongly aggregated, with a few of the occupied trees hosting hundreds of woodwasps. Nematode parasitism was positively associated with *S. noctilio* density, and negatively associated with the density of rhyssine parasitoids. Parasitism by the parasitoid *Ibalia leucospoides* was positively associated with host (*S. noctilio*) density, while parasitism by the rhyssine parasitoids was negatively associated with density of *S. noctilio*. Thus, most *S. noctilio* come from a few attacked trees in a forest, and *S. noctilio* from those high-density trees experienced high parasitism by both the invasive nematode and the most abundant native parasitoid, *I. l. ensiger*. There is little evidence for direct competition between the nematodes and parasitoids. The negative association occurring between rhyssine parasitoids and *I. l. ensiger* suggests rhyssines may suffer from competition with *I. l. ensiger* which parasitize the host at an earlier life stage. In addition to direct competition with the native woodwasp *Sirex nigricornis* for suitable larval habitat within weakened trees, the large *S. noctilio* population increases the parasitoid and nematode populations, which may increase parasitism of *S. nigricornis*.

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Keywords
Aggregation, co-infection, competition, *Deladenus*, density dependence, forest pest, *Ibalia*, parasite community, pine, *Rhyssa*, *Sirex noctilio*, spillback

Introduction

In any community there are multiple parasite species simultaneously associated with any host species (Shaw and Dobson 1995; Pedersen and Fenton 2007). Parasites share hosts by infecting different individuals in host populations and by co-infecting the same host individuals. Thus, interactions among parasites occur indirectly due to exploitative competition for shared hosts or directly through interaction outside the host (Ode et al. 2021), as well as within host individuals (van Nouhuys and Punju 2010; Harvey et al 2013). Because parasite species are each independently sensitive to host density, the strengths of their interactions with each other and with hosts can change with host density. The resulting interactions influence the population dynamics of both parasites and hosts, affecting the composition and structure of communities (Settle and Wilson 1990; Telfer et al. 2010; Holt and Bonsall 2017).

Invasive species may act as consumers, competitors, hosts to existing parasites, and as parasites of existing hosts. The introduced species may have a greater prevalence than in their native range (Callaway and Aschehoug 2000; Wolfe 2002), and their invasion can have a strong effect on the structure of native communities (Mitchell et al. 2006; Kelly et al. 2009; Kenis et al. 2009). The roles of multiple parasites, both native and introduced, in these new composite communities are understudied (Sarabeev et al. 2022) and complex (Dunn et al 2012; Llopis-Belenguer et al. 2020). For instance, in the northeastern US, the invasive spongy moth, *Lymantria dispar*, interacts with two pathogens and numerous parasitoid species that have been accidentally and intentionally introduced (Fuester et al. 2014), resulting in many complex interspecific dynamics (Hajek and van Nouhuys 2016).

Larvae of the Eurasian woodwasp *Sirex noctilio* (Siricidae) develop in the xylem of pine trees in association with a symbiotic white rot fungus, *Amylostereum areolatum*, that assists in slowly killing attacked trees and acting as an external rumen for larvae (Hajek and Castrillo 2021; Gruner and Thompson 2021). In North America, this invasive woodwasp was first found to be established near Lake Ontario in New York state in 2004 and has been spreading since then (Liebhold and Hajek 2021). *Sirex noctilio* has previously invaded and caused severe damage in pine plantations in the Southern Hemisphere, where pines are not native (Hurley et al. 2007). In North America, where pines are native, *S. noctilio* often successfully develops within trees that are already suppressed or weakened (Dodds et al. 2010; Foelker and Haavik 2021). Native *Sirex* species in North America and their associated parasite communities were already present when *S. noctilio* arrived. In particular, in eastern North America, the native *Sirex nigricornis* and associated parasitoids and nematodes already infested weakened pine trees (Table 1). Since its introduction, *S. noctilio* has been found to develop within the

Table 1. Members of the North American *Sirex* community associated with *Pinus* in this study, made up of invasive and native species and their origins. Invasives are listed in bold.

Species	Origin
Woodwasps (Siricidae)	
Sirex noctilio	**Eurasia**
Sirex nigricornis	Eastern North America
Parasitoids (Hymenoptera)	
Ibaliidae	
Ibalia leucospoides ensiger	Eastern North America
Ichneumonidae	
Rhyssa lineolata	Eastern North America
Rhyssa persuasoria	Eastern North America
Rhyssa crevieri	Eastern North America
Megarhyssa nortoni	Eastern North America
Pseudorhyssa nigricornis	Eastern North America
Parasite (Nematoda)	
Neotylenchidae	
***Deladenus siricidicola* INA**	**Eurasia** (not North America)
Sirex symbiont/*Deladenus* food (Fungus)	
Russulales	
Amylostereum areolatum	North America + **Eurasia**

same pines as *S. nigricornis* (e.g., Hajek et al. 2013, 2017) and is attacked by the same species of hymenopteran parasitoids (Foelker et al. 2016a, b) and parasitic nematodes (Morris et al. 2013; Haavik et al. 2016) (Table 1).

The community of parasitoids associated with *S. noctilio* and *S. nigricornis* in eastern North America is composed of up to six native hymenopteran species. *Ibalia leucospoides ensiger* (Ibaliidae) parasitizes eggs/early instars and is almost always the most common species. Four species of rhyssines (Ichneumonidae) parasitize later larval instars, and *Pseudorhyssa nigricornis* (also Ichneumonidae) is a kleptoparasitoid attacking the rhyssines (Foelker and Parry 2021) (Table 1). The biologies of these native parasitoid species are not well understood, although molecular analyses have shown that the rhyssines (analyzed as a group) and *I. l. ensiger* parasitize both *S. nigricornis* and *S. noctilio* (Foelker et al. 2016b).

The dimorphic nematode, *Deladenus siricidicola*, is also a parasite of *S. noctilio*. The impact of nematodes on host woodwasps is determined by both nematode and woodwasp species and genotypes (Bedding 1972). Different species and strains of *Deladenus* parasitizing differing species and strains of *Sirex* are known to either totally sterilize (i.e., kill all host eggs in adult females), partially sterilize, or not sterilize parasitized hosts (van Nouhuys et al. 2022). The INA (= Introduced to North America; formerly referred to as 'non-sterilizing') strain of *D. siricidicola* that was putatively accidentally introduced with *S. noctilio* to North America does not sterilize eggs of *S. noctilio* but causes a decrease in adult size and fecundity (Kroll et al. 2013; Hajek and Morris 2021). *Deladenus siricidicola* also occurs as a free-living mycophagous form that feeds on the *Sirex*-symbiotic fungus within infested pines. Several strains of *S. noctilio* have been introduced to North America from unknown sources and origins (Boissin et

al. 2012; Bittner et al. 2017), and the INA strain of *D. siricidicola* is also from an unknown source, probably within the native distribution of *S. noctilio* (Morris et al. 2020). A native dimorphic nematode in pines, *Deladenus proximus*, described originally as a parasite of *S. nigricornis* (Bedding 1974), is never (Kroll et al. 2013; Haavik et al. 2016) or only rarely (Morris et al. 2013) recorded parasitizing *S. noctilio*.

Invasive *S. noctilio* in northeastern North America is therefore attacked by numerous species of native parasitoids as well as an introduced parasitic nematode (Table 1). This woodwasp species did not co-evolve with these parasitoids and it is questionable whether *S. noctilio* in any tree might have co-evolved with the nematode strain within that tree. Regardless, these natural enemies occupy the same community and rely on the same host as a resource, with the parasitoids killing woodwasps as they develop and nematodes living as internal parasites in *S. noctilio* larvae and adults.

Our overall goal in this study was to investigate relations among the parasitic nematode, the native parasitoid community, and the invasive host woodwasp in naturally occurring attacked trees. We evaluated emergence from 204 *S. noctilio*-infested trees from multiple forested areas in northeastern North America between 2011 and 2019. We tested the hypotheses that *S. noctilio* aggregate within a few of the infested trees in a stand, and that the natural enemies would each respond positively to host density. Further, since the natural enemies co-occur but cannot all successfully infect the same host individuals, there would be negative associations among them where their densities were high enough for competition to occur. Given the patterns of tree infestation and parasitism that we found, we discuss likely consequences to populations of the native woodwasp *S. nigricornis* from invasion of this community by *S. noctilio*. Results from this study will improve our understanding of population level interactions in mixed invasive and native communities, as well as the ecology of this host/parasite community, as the invasive host continues to expand its range in North America.

Materials and methods

Between 2010 and 2018, 204 *S. noctilio*-infested pines were identified at sites where active infestations of *S. noctilio* were known or hypothesized to be present in pine forests at 21 sites in New York and Pennsylvania, USA (Table 2). Detection generally occurred from October to December. Nearly all of the pines were *Pinus resinosa*. Infested trees were patchily distributed within the forest stands. When searching for infested trees, trunks were inspected to 3 m for resin beads as these are indications of infestation (Haavik and Foelker 2021). In spring 2011–2019, before *S. noctilio* emergence, the trees that had been identified as infested were felled and areas of the trunks with resin beads were cut into 70 cm long bolts. Insects were reared from this wood and collected as they emerged, as described in Hajek et al. (2017). Throughout, the years presented for samples are the years in which emergence occurred.

Sirex and parasitoid adults that emerged were kept individually in vials at 4 °C. *Sirex noctilio* and *S. nigricornis* were identified using Schiff et al. (2006, 2012) and

Table 2. Localities of collections of *Sirex*-infested trees in New York state and Pennsylvania.

Year	State	County	Site*	*Pinus* species	GPS	No. trees
2011	New York	Schuyler	Arnot Forest	*P. sylvestris*	42.26445, -76.62757	2
2011	Pennsylvania	Tioga	TSF: Government Rd	*P. resinosa*	41.65038, -76.92572	9
2011	Pennsylvania	Tioga	TSF: Mountain Ridge Rd	*P. resinosa*	41.74501, -76.94507	6
2011	New York	Cortland	Heiberg Forest	*P. resinosa*	42.76094, -76.08341	2
2011	New York	Tompkins	Waterburg Rd	*P. resinosa*	42.49939, -76.67325	3
2011	New York	Broome	Triangle	*P. resinosa*	42.34022, -75.88022	1
2012	New York	Schuyler	Arnot Forest	*P. resinosa*	42.26445, -76.62757	9
2012	New York	Tompkins	Danby	*P. sylvestris*	42.37903, -76.47251	1
2012	New York	Steuben	Cameron State Forest	*P. resinosa*	42.26578, -77.41622	1
2012	New York	Schuyler	Finger Lakes National Forest	*P. resinosa*	42.47374, -76.77994	3
2012	New York	Warren	Nr. Pack Forest	*P. resinosa*	43.51550, -73.81478	6
2012	Pennsylvania	Tioga	TSF: Government Rd	*P. resinosa*	41.65038, -76.92572	14
2012	Pennsylvania	Tioga	Hills Creek State Park	*P. resinosa*	41.85348, -77.19989	11
2012	Pennsylvania	Tioga	TSF: Hypocrite Trail	*P. resinosa*	41.67096, -76.92317	18
2012	Pennsylvania	Tioga	Leonard Harrison State Park	*P. resinosa*	41.69646, -77.45460	5
2013	Pennsylvania	Tioga	TSF: Hypocrite Trail	*P. resinosa*	41.67096, -76.92317	12
2013	Pennsylvania	Tioga	Hills Creek State Park	*P. resinosa*	41.85348, -77.19989	5
2013	Pennsylvania	Tioga	Leonard Harrison State Park	*P. resinosa*	41.69646, -77.45460	2
2014	New York	Schuyler	Arnot Forest	*P. resinosa*	42.28194, -76.63138	2
2014	Pennsylvania	Tioga	Hills Creek State Park	*P. resinosa*	41.85348, -77.19989	26
2014	New York	Cortland	Hewitt State Forest	*P. resinosa*	42.74353, -76.22174	2
2015	Pennsylvania	Tioga	TSF: Arnot Forest	*P. resinosa*	41.67380, -77.14184	4
2015	New York	Schuyler	Arnot Forest	*P. resinosa*	42.28194, -76.63138	1
2015	Pennsylvania	Tioga	TSF: Fellows Creek	*P. resinosa*	41.69965, -76.96671	5
2015	Pennsylvania	Tioga	Hills Creek State Park	*P. resinosa*	41.85348, -77.19989	13
2015	Pennsylvania	Tioga	Ridge Road	*P. resinosa*	41.67589,-76.95881	1
2015	New York	Oneida	Sand Flats State Forest	*P. sylvestris*	43.55212, -75.27708	3
2015	Pennsylvania	Tioga	TSF: Tanglewood	*P. resinosa*	41.71145, -76.98356	4
2016	Pennsylvania	Tioga	TSF: Hypocrite Trail	*P. resinosa*	41.67096, -76.92317	3
2017	Pennsylvania	Clarion	Corsica	*P. sylvestris*	41.17809, -79.22653	10
2017	Pennsylvania	Indiana	Hillsdale	*P. resinosa*	40.75009, -78.88494	10
2017	Pennsylvania	Tioga	TSF: Hypocrite Trail	*P. resinosa*	41.67096, -76.92317	3
2019	Pennsylvania	Tioga	TSF: Government Rd.	*P. resinosa*	41.65038, -76.92572	3
2019	Pennsylvania	Tioga	TSF: Hypocrite Trail	*P. resinosa*	41.67096, -76.92317	4

*TSF = Tioga State Forest

associated parasitoids were identified using Standley et al. (2012). In 2011, we were unable to distinguish between some rhyssines, and the rhyssines emerging in 2012 were not all identified, so these are listed as *Rhyssa* spp. (Suppl. material 1).

To evaluate nematode parasitism, subsamples of *S. noctilio* from each site and year were dissected as described in van Nouhuys et al. (2022) and presence of parasitic nematodes within bodies was recorded. A total of 3154 randomly chosen *S. noctilio* were dissected to detect whether they were parasitized by nematodes. Species of nematodes were not evaluated using molecular methods for this study but, based on past results (Kroll et al. 2013; Williams and Hajek 2017), we presume that the vast majority

of parasitic nematodes were *D. siricidicola* INA. Another nematode species, *Deladenus proximus*, is primarily known from *S. nigricornis* hosts. *Deladenus proximus* was reported parasitizing a few *S. noctilio* collected in New York state in 2010 (Morris et al. 2013). However, *D. proximus* are usually found in the host eggs (Hartshorn 2021; van Nouhuys et al. 2022), and in our study nematodes were only seen within eggs from 4 *S. noctilio* from 2 sites in 2011. This was the first year of this study and there *S. nigricornis* were more abundant (Suppl. material 1).

Data analysis

Sirex density was quantified as all of the emerged *Sirex* plus each emerging *Sirex* parasitoid, as each parasitoid is solitary, representing one host individual. The native woodwasp *S. nigricornis* emerged from 25 of the 204 trees in five of the eight years. From 22 of these trees, *S. noctilio* emerged as well, usually in much higher quantities than *S. nigricornis*. From the remaining three trees only *S. nigricornis* emerged. As *S. noctilio* had emerged from other trees from those sites sampled throughout the same years and the parasitoids use both *Sirex* species as hosts (Foelker and Parry 2021), these trees were included in the study. *Sirex nigricornis* individuals that emerged were included in the *Sirex* density estimates because they are hosts to both the parasitoids and the nematode (Morris et al. 2013). For the statistical analyses involving the rhyssines all five species were combined because no one species was common enough for separate analysis, and because in some cases the individual species were not differentiated (Suppl. material 1).

All statistical analyses were done using JMP (SAS Institute Inc. 2021). For the analysis of aggregation of *Sirex* among trees we compared the distribution of samples among trees within a site with a Poisson distribution which is what is expected if the wasps were independent and equally likely to emerge from any of the sampled trees. The statistical comparison among counts per tree was done using a Poisson dispersion test (Spinelli and Stephens 1997) for the 12 sites in which 6 or more trees were sampled within a year. Sites with fewer trees provided too little data on tree-to-tree distribution to meaningfully conduct such tests.

For the analysis of the association of nematode infection with per tree *Sirex* density and rate of parasitism by parasitoids we used logistic regression. The response variable was the presence/absence of nematodes in each of the 3154 *S. noctilio* dissected to detect nematodes. The samples collected from 2012 were not included because very few *S. noctilio* were dissected that year. The explanatory variables were year, site nested in year where sites were sampled across multiple years, the log of the number of *Sirex* in the tree the sample came from, the fraction of hosts parasitized by *I. l. ensiger* and by the combined rhyssine parasitoids in that tree, and interactions between the host and each parasitoid, and between *I. l. ensiger* and the combined rhyssines. Interactions that did not contribute to the model were removed. Because the number of wasps (*Sirex* + parasitoids) per tree ranged widely (from 1 to 864), with many trees occupied by few wasps, the number of wasps was log-transformed. Because the different parasitoids

may have different patterns of parasitism and potential associations with the nematode, we separated *I. l. ensiger* and the combined rhyssine parasitoids.

For the analysis of association of parasitism by parasitoids with woodwasp density at the tree level, we used logistic regression with the full data set of all 204 trees that wasps emerged from over all eight years. Three separate models were tested. The binomial response variable in the first was whether a sample was a parasitoid or *Sirex*. In the second model the response variable was whether the sample was *I. l. ensiger* or not (if not *I. l. ensiger* it could be a *Sirex* or a rhyssine). In the third model the response variable was whether the sample was a rhyssine or not (if not a rhyssine it could be *Sirex* or *I. l. ensiger*). The explanatory variables in all three models included year, site nested in year, and the log of the number of *Sirex* in the tree the sample came from (host density). Since each parasitoid can have an independent relationship to host density, in the model for total parasitism the per tree rates of parasitism by *I. l. ensiger* and rhyssines, as well as their interactions with host density, were included as explanatory variables. The model for *I. l. ensiger* included the per tree rate of parasitism by rhyssines, and its interaction with host density as response variables. The model for rhyssines included per tree rate of parasitism by *I. l. ensiger*, as well as the interaction of *I. l. ensiger* parasitism and host density as response variables.

Results

Between 2011 and 2019, *S. noctilio* and their parasitoids were reared from 204 *S. noctilio*-infested trees from Pennsylvania and New York State (Table 2). There were 9852 adult woodwasps or parasitoids that emerged over the eight years of sampling. Of these, 3870 were parasitoids, 5804 were *S. noctilio*, and 178 were the native woodwasp *S. nigricornis* (Suppl. material 1). Most trees (130 of 204, 63.7%) were infested with 1–25 *Sirex* (adult *Sirex* + their parasitoids). However, 45.7% of the population occupied 12 of 204 trees. These trees each contained more than 198 *S. noctilio*, with 854 individuals emerging from the tree with the highest occupancy (Fig. 1). Thus, the distribution of *Sirex* equivalents (adult *Sirex* + their parasitoids) among trees was strongly aggregated, differing significantly from the expected Poisson distribution that would occur if they were distributed randomly among infested trees. This is true for the combined data (χ^2 = 1700.34; $P < 0.0001$) (Fig. 1), as well as in each of 12 sites analyzed separately (χ^2 ranged from ≈ 0.00 to χ^2 = 121.34, all are $P < 0.0001$). The distributions of individuals among trees in the six sites with the highest densities are presented in Fig. 2.

Overall, 39% of the *Sirex* were parasitized by parasitoids. The most abundant parasitoid species was *I. l. ensiger*, which comprised 81% of the parasitoids reared and was found at every site. Next most abundant was *Rhyssa lineolata*, which made up 63% of the rhyssines (leaving out samples from 2012 when rhyssine species were not separated, Suppl. material 1) and was also found at every site, although densities were always less than *I. l. ensiger*. The other four rhyssines (two *Rhyssa* species: *R. persuasoria* and

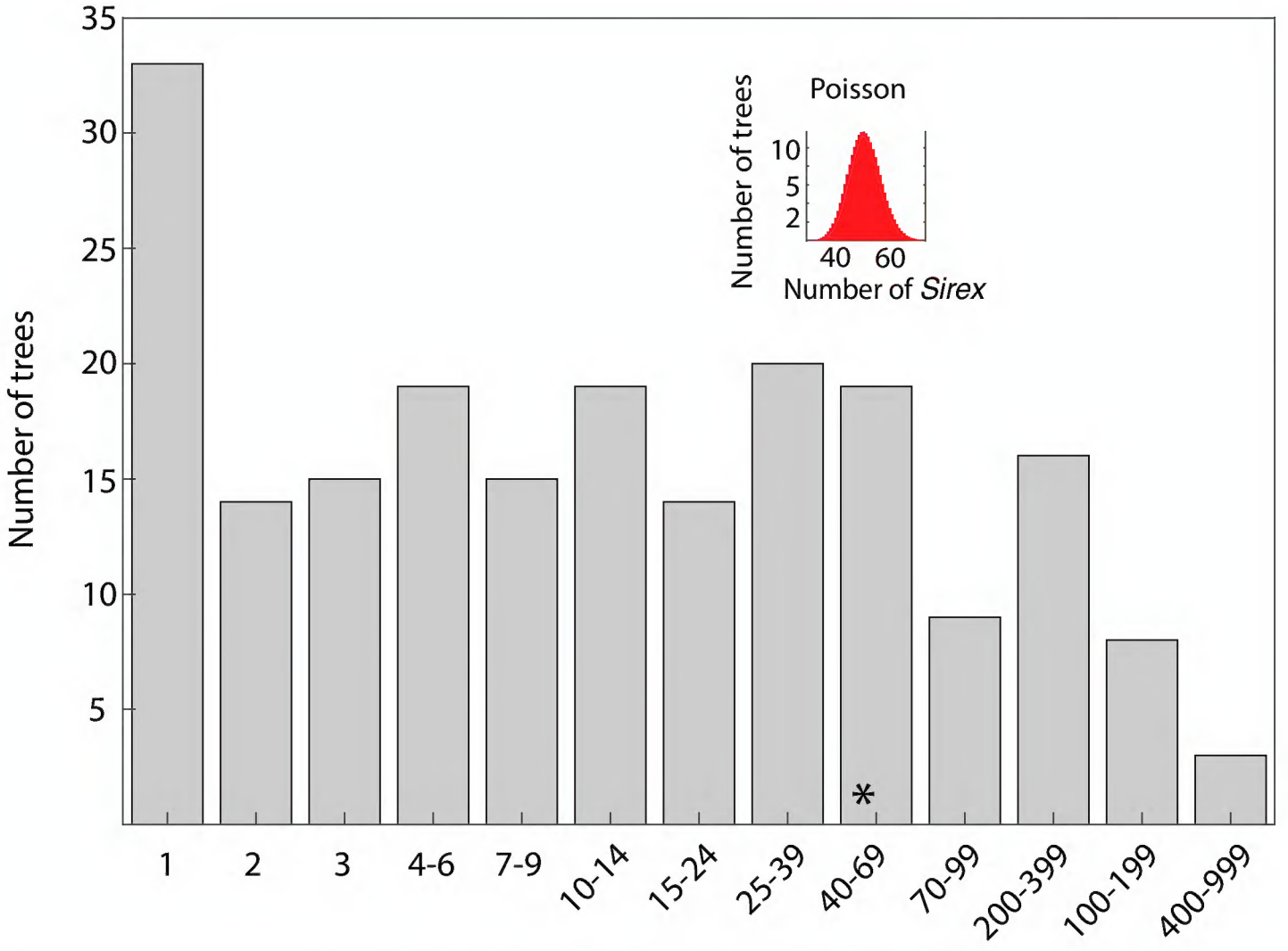

Figure 1. The distribution of *Sirex* equivalents (*Sirex* adults + parasitoid adults) emerging from trees in the whole data set. The inset shows the distribution of *Sirex* equivalents among the same number of trees if the *Sirex* were distributed randomly among trees (a Poisson distribution). The * indicates the mean number of wasps per tree (48.3). The number of wasps along the x-axis is shown in a modified log scale in order to make both small and large numbers of wasps per tree visible.

R. crevieri, *Megarhyssa nortoni*, and the kleptoparasitoid *Pseudorhyssa nigricornis*) occurred much less commonly. The 8 collected *M. nortoni* came from three sites in the years 2011 and 2013. Most of the 13 *P. nigricornis* came from Hypocrite Trail in Tioga State Forest (Pennsylvania), in two different years (Suppl. material 1).

Nematodes were found in 11% of the dissected *S. noctilio*. The proportion of nematode-parasitized hosts in a tree was positively associated with host density ($\chi^2 = 4.92$; $P = 0.0265$; Table 3a; Fig. 3a). There was no association with parasitism by *I. l ensiger* ($\chi^2 = 0.004$; $P = 0.9460$; Table 3a), but a negative association occurred with parasitism by the rhyssine parasitoids ($\chi^2 = 31.57$; $P < 0.0001$; Table 3a; Fig. 3b). This was especially true at low host densities ($\chi^2_{\textit{rhyssines x host density}} = 21.67$; $P = 0.0001$; Table 3a). Nematode parasitism also differed between years ($\chi^2 = 166.04$; $P < 0.0001$; Table 3a), as well as among sites within years ($\chi^2 = 329.13$; $P < 0.0001$; Table 3a). For instance, only 7% of hosts dissected from the Corsica and Hillsdale, PA sites sampled in 2017

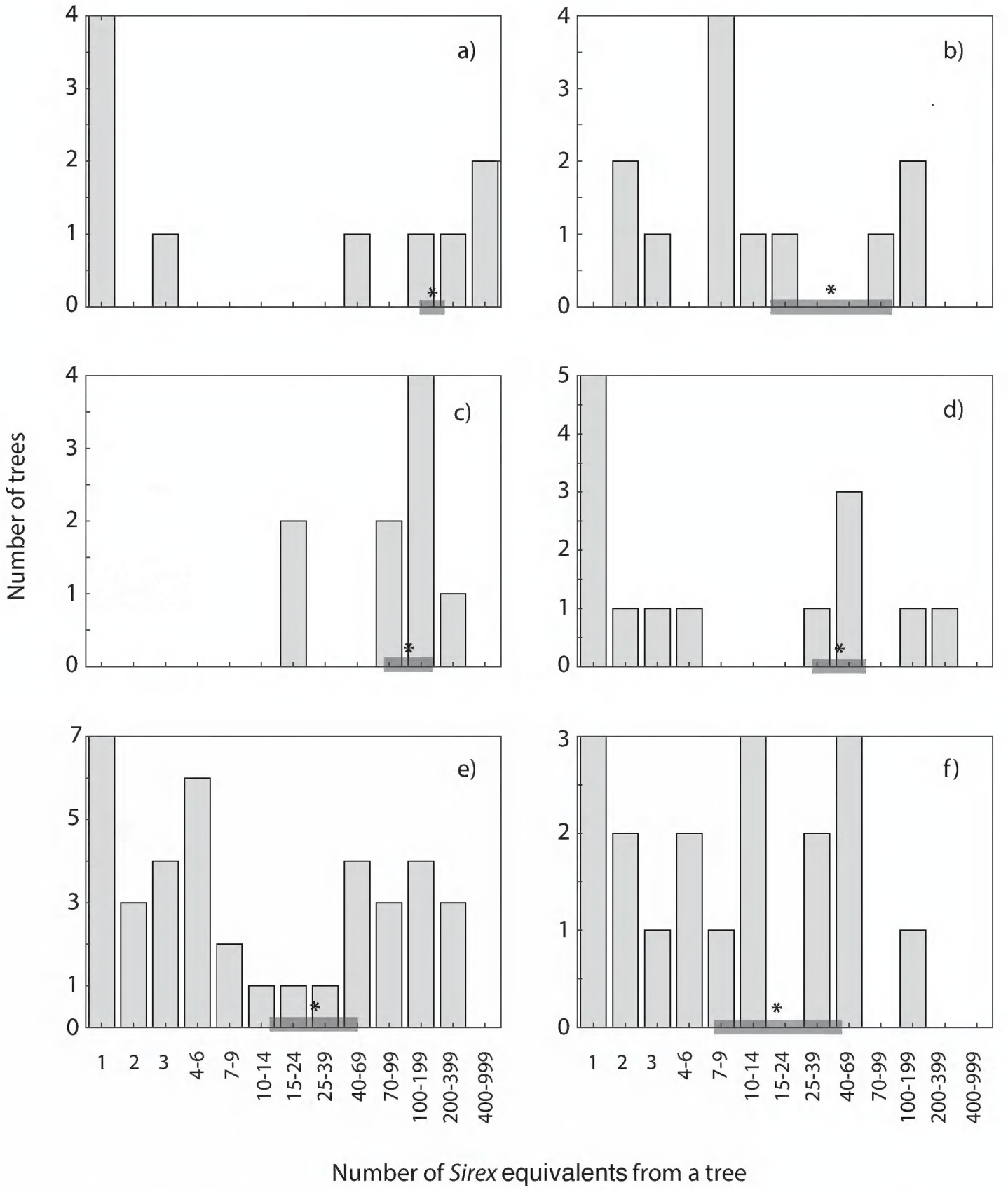

Figure 2. The distribution of *Sirex* equivalents (*Sirex* adults + parasitoid adults) emerging from the 6 sites with the most data (each had 398 or more *Sirex* equivalents and nine or more trees). The wasps were strongly aggregated in these and the other 6 sites tested (see text). * denotes the mean number of *Sirex* equivalents per tree. The horizontal gray bars represent the 95% CI range of wasps per tree if the *Sirex* were distributed randomly among the trees, which would be a Poisson distribution (as shown in the inset in Fig. 1). The number of wasps along the x-axis is shown in a modified log scale to make both small and large numbers of wasps visible. a) 2017 Hillsdale site, 2052 *Sirex* equivalents from 10 trees, b) 2013 Hypocrite Trail site, 400 *Sirex* equivalents from 12 trees, c) 2011 Government Rd. site, 1058 *Sirex* equivalents from 9 trees, D) 2012 Government Rd. site, 575 *Sirex* equivalents from 14 trees, e) 2014 Hypocrite Trail site, 2055 *Sirex* equivalents from 39 trees, f) 2012 Hypocrite Trail site, 398 *Sirex* equivalents from 18 trees.

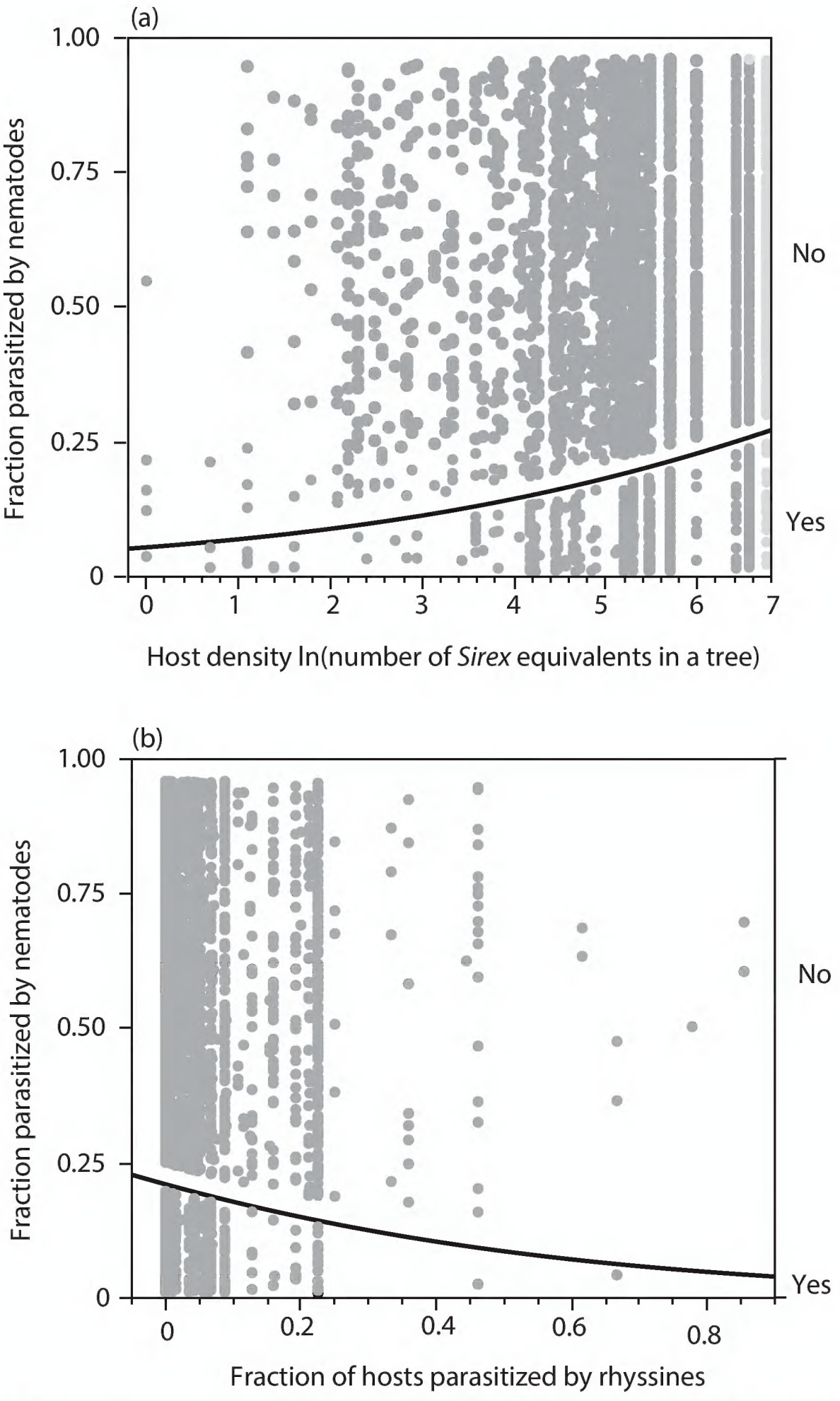

Figure 3. The association of parasitism by the nematode *Deladenus siricidicola* with **a** per tree *Sirex* density (Logistic regression model coefficient $P < 0.026$; Table 3a) and **b** fraction of *Sirex* in the tree parasitized by rhyssines (Logistic regression model coefficient $P < 0.0001$; Table 3c). Each point represents a dissected *S. noctilio*. The points are distributed vertically in order to show the amount of data at each host density. The points below the curves are parasitized *D. siricidicola* (Yes) and the points above the curve are not (No). See the text for explanation of the statistical models.

Table 3. Results of the logistic regression analyses of a) nematode parasitism, and parasitism by b) all parasitoids, c) *I. I. ensiger*, and d) rhyssines. See text for details of models.

Parameter	df	Estimate(SE)	χ^2	$P > \chi^2$	Odds ratio	Effects likelihood ratio χ^2	$P > \chi^2$
a) Nematodes							
Year	6	multiple				166.04	<0.0001
Site (Year)	20	multiple				329.13	<0.0001
Host density*	1	0.23(0.10)	4.72	0.0298	1.26	4.92	0.0265
Rhyssines rate**	1	-5.81(1.14)	26.15	<0.0001	0.01	31.57	<0.0001
Rhyssines rate × host density	1	5.05(1.20)	17.66	<0.0001		21.67	<0.0001
I. I. ensiger rate	1	-0.04(0.58)	0.00	0.9460	0.97	0.004	0.9460
b) All parasitoid wasps							
Year	7	multiple				1.25	0.9898
Site (Year)	26	multiple				13.48	0.9793
Host density	1	-0.002(0.03)	0.00	0.9522	0.99	0.003	0.9522
I. I. ensiger rate	1	4.62(0.26)	321.88	<0.0001	101.72	348.39	<0.0001
I. I. ensiger rate × host density	1	-0.29(0.16)	3.21	0.0734		3.34	0.0674
Rhyssines rate	1	4.65(0.26)	283.23	<0.0001	105.37	316.39	<0.0001
Rhyssines rate × *I. I. ensiger* rate	1	-3.29(1.31)	6.30	0.0121		6.46	0.0110
c) *I. I. ensiger*							
Year	7	multiple				17.68	0.0135
Site (Year)	26	multiple				211.78	<0.0001
Host density	1	0.18(0.03)	30.51	<0.0001	1.19	31.88	<0.0001
Rhyssines rate	1	0.42(0.24)	3.07	0.0797	1.51	3.04	0.0813
Rhyssines rate × host density	1	1.16(0.16)	53.44	<0.0001		62.39	<0.0001
d) Rhyssines							
Year	7	multiple				422.98	<0.0001
Site (Year)	26	multiple				256.20	<0.0001
Host density	1	-0.22(0.59)	13.52	0.0002	0.80	12.60	0.0004
I. I. ensiger rate	1	0.71(0.41)	3.00	0.0830	2.04	3.00	0.0832
I. I. ensiger rate × host density	1	1.92(0.23)	72.32	<0.0001		82.44	<0.0001

*For each statistical model Host density is the log of the number of *Sirex* equivalents emerging from a tree.
** For each statistical model Rate is the fraction of *Sirex* parasitized by *I. I. ensiger* or Rhyssines within a tree.

were parasitized by nematodes, whereas 82% of hosts dissected at the Tanglewood, PA site in 2015 were parasitized by nematodes (Fig. 4).

Overall parasitism by parasitoids was unrelated to tree-level host density ($\chi^2 = 0.003$; $P = 0.9522$; Table 3b). However, parasitism by *I. l. ensiger* increased with host density ($\chi^2 = 31.89$; $P < 0.0001$; Table 3c; Fig. 5a), while parasitism by the rhyssines decreased with host density ($\chi^2 = 12.60$; $P = 0.0004$; Table 3d; Fig. 5b). Parasitism by *I. I. ensiger* had no overall association with rate of parasitism by the rhyssines ($\chi^2 = 3.04$; $P = 0.0813$; Table 3c), except at low host densities where rhyssine parasitism was high ($\chi^2_{rhyssines \times ln(host)} = 62.39$; $P = < 0.0001$; Table 3c). Similarly, parasitism by the rhyssines also had no overall association with rate of parasitism by *I. l. ensiger* ($\chi^2 = 3.00$; $P = 0.0832$; Table 3d), except at low host density ($\chi^2_{I.\ l.\ ensiger \times ln(host)} = 82.44$; $P = < 0.0001$; Table 3d). Parasitism by *I. l. ensiger*, rhyssines, and total parasitism each differed significantly among years and among sites (Table 3b, c, d).

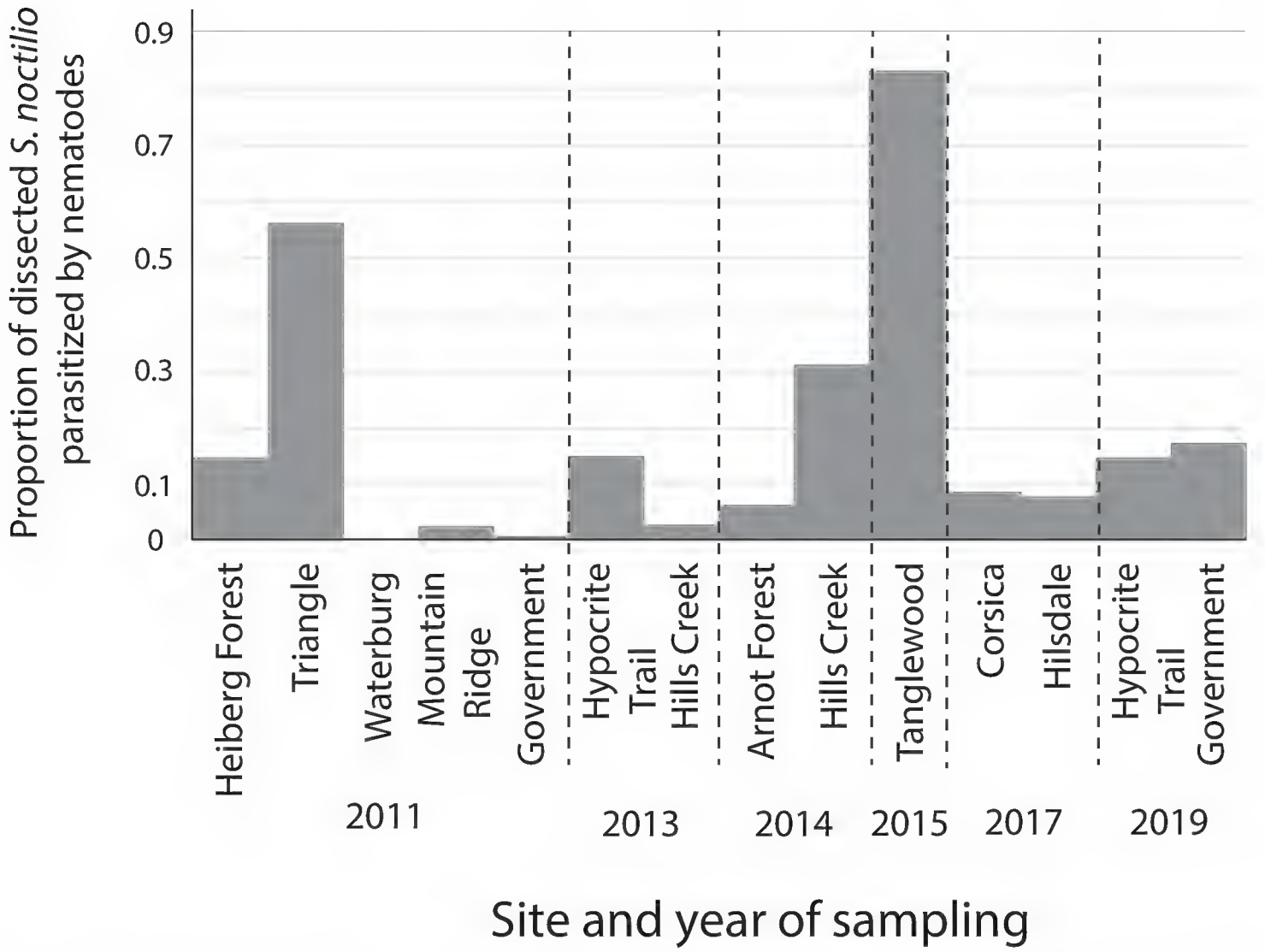

Figure 4. The proportions of dissected *S. noctilio* parasitized by *D. siricidicola* at each site between 2011 and 2019. Sites with fewer than 10 dissected *S. noctilio* are excluded as well as all sites from 2012.

Discussion

The invading *S. noctilio* exhibited very strong aggregation in specific trees within a stand, with up to 854 *Sirex* equivalents emerging from one tree and few *S. noctilio* emerging from the majority of infested trees (Figs 1, 2). In North America, Krivak-Tetley et al. (2022) and Haavik et al. (2018) reported a similar pattern of higher densities in few trees with lower densities in most. In Galicia, Spain, where *S. noctilio* is native, the pattern of aggregated emergence also occurred in pine plantations although the overall population was lower and the maximum emerging from one tree was 50 *S. noctilio* (Lombardero et al. 2016).

Generally, aggregated resource use can result from variation of resource quality (Woodcock et al. 2002), host susceptibility (Poulin 2013), or behavioral attraction to conspecifics (Cronin and Strong 1999). In this case, woodwasps are often attracted to weakened pines that are more susceptible to attack (Haavik and Foelker 2021); the occurrence of weakened trees can be a limiting and ephemeral resource for woodwasps. Additionally, *S. noctilio* females are attracted to the odor of the *Sirex*-associated fungal symbiont (Sarvary et al. 2015; Faal et al. 2021). Thus, *S. noctilio* may be strongly attracted to trees with many *Sirex* because those trees would already have been colonized by the *Sirex*-symbiotic fungus.

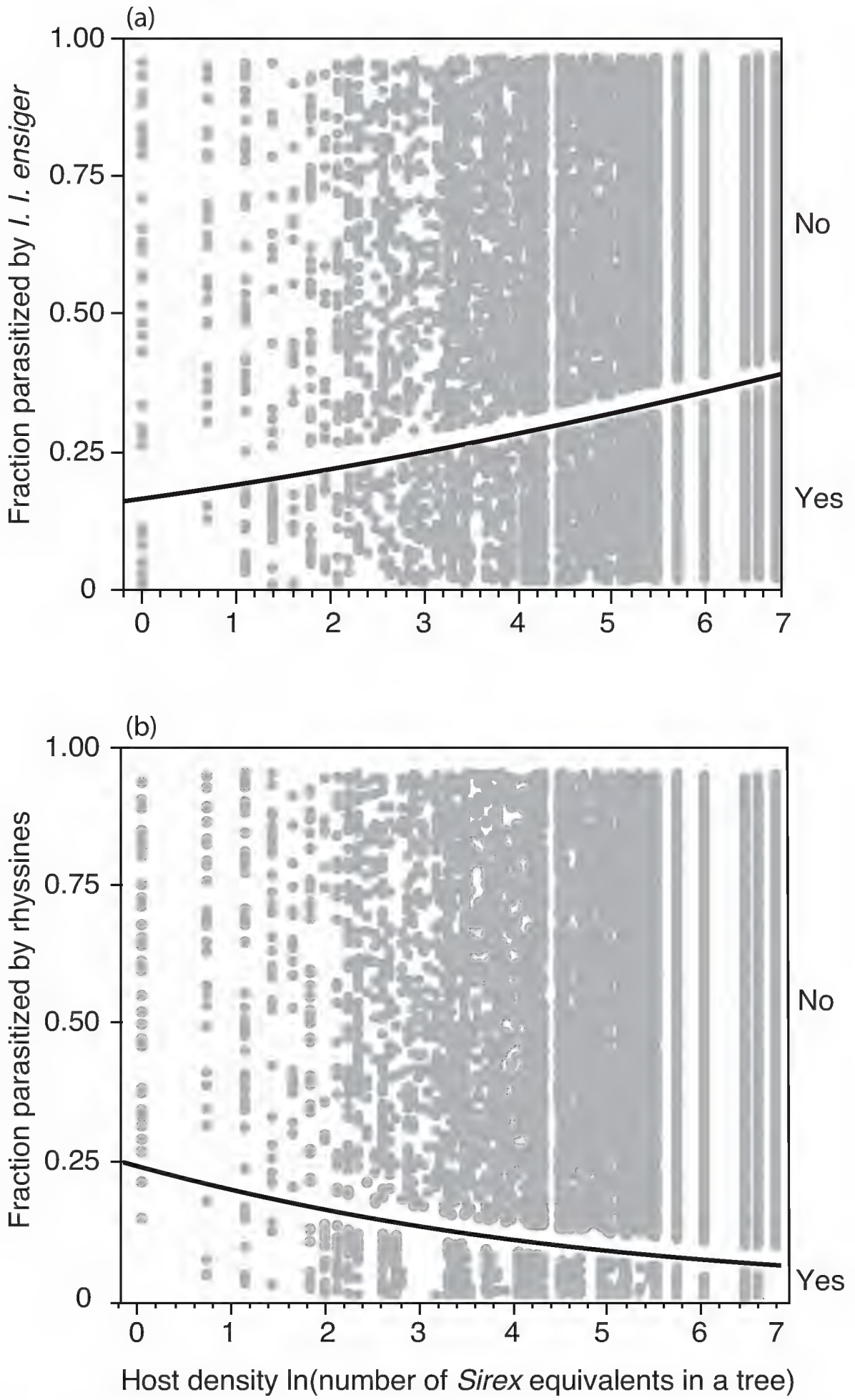

Figure 5. The association of parasitism by parasitoids with tree level host density. The curves show the logistic fit for **a** *I. l. ensiger* ($P < 0.0001$; Table 3c) and **b** rhyssines ($P = 0.0004$; Table 3d). The horizontal axis shows host density as the log of the number of *Sirex* equivalents (adult *Sirex* + all parasitoids) emerging from a tree. Each data point is one sample. The points are distributed vertically in order to show the amount of data at each host density. The points below the curve are parasitoids (Yes) **a** *I. l. ensiger* and **b** rhyssines, and the points above the curve are unparasitized *Sirex* (No). See text for explanation of the statistical models.

The nematode *D. siricidicola* was present in 11% of the *S. noctilio* which is less than reports from many smaller studies in North America (see Krivak-Tetley et al. 2022), though nematode parasitism levels were variable and were much higher in some sites (Fig. 4). The fraction of samples in a tree that were parasitized by *D. siricidicola* increased strongly with host density (Fig. 3a). This is in contrast to the negative association found by Kroll et al. (2013) when studying fewer trees (n = 25) over one year. Positive host density dependence could result from a higher chance of nematode-infected females ovipositing in the same trees as healthy females at high density. Additionally, spread of the nematode among woodwasps within trees would be facilitated by high host densities. One reason for this is that high woodwasp density would result in high densities of the fungus *A. areolatum*, which is eaten by these nematodes when they are mycophagous. More *A. areolatum* throughout trees would potentially facilitate greater dispersal by the mycophagous-phase nematodes within trees, which would result in more nematodes reaching and parasitizing *Sirex* larvae.

Nematodes may parasitize a woodwasp before or after it has been parasitized by a wasp. Once within a shared host, nematodes could, in principle, move from the woodwasp larva to a parasitoid larva. However, the nematode *D. siricidicola* is specific to *Sirex* as well as parasitizing a wood-dwelling genus of beetle associated with siricids (*Serropalpus*) (Bedding and Akhurst 1978; Bittner et al. 2016). Other species of parasitic nematodes have been reported from rhyssines in other locales (Bedding and Akhurst 1978). However, Morris et al. (2020) evaluated 388 adult rhyssines emerging from pines between 2012–2015 in the same research area that we studied and found no nematodes in them. Thus, we do not believe that *D. siricidicola* in this study were parasitizing the parasitoids.

Further, the nematode *D. siricidicola* cannot successfully develop in or be vectored by a *Sirex* parasitized by a parasitoid because the host is killed by the parasitoid. While the nematodes would not succeed in such a shared host, parasitoids likely can develop in *Sirex* larvae that are also parasitized by nematodes. There may be a cost to parasitoids due to reduced host size since nematode-parasitized *Sirex* are somewhat smaller than unparasitized individuals (Hajek and Morris 2021). Additionally, nematode infection has been shown in some systems to increase host immune response, including parasite encapsulation (Castillo et al. 2011), which could reduce the success of parasitoids. Alternatively, immune suppression by the nematode combined with immune suppression due to the parasitoid venom could be detrimental to the host, causing it to die or to have greater susceptibility to other parasites (Shaik et al. 2020). Nonetheless, we expect that when the nematode *D. siricidicola* and a parasitoid are using the same host individual, the parasitoid would be the superior competitor. We found that parasitism by nematodes was neither positively nor negatively associated with parasitism by the abundant parasitoid *I. l. ensiger* (Fig. 3b), but it was negatively associated with parasitism by the rhyssines (Fig. 3c).

The observed negative association of nematode parasitism with rhyssines may simply be because the nematodes are strongly positively host density dependent, so they are nearly absent from trees with low host density, which are the ones in which

parasitism by rhyssines was highest. Alternatively, competition between nematodes and rhyssines at low host densities may decrease the number of nematode-infected *Sirex*, contributing to the pattern of host density dependence of the nematodes. While such competition may contribute to the pattern, it is not the full explanation because at low host density nematode parasitism is near 0 (Fig. 3a), and rhyssine parasitism reaches only 24% (Fig. 5b).

Both the nematode and the abundant parasitoid *I. l. ensiger* increase with host density within trees. Yet there is no evidence of direct competition, since even accounting for host density, high *I. l. ensiger* density was not associated with lower prevalence of nematodes. This suggests that there could be some spatial segregation of host use. For example, *I. l. ensiger*, which have short ovipositors, have been found to be most abundant high up in trees where bark is thinner (Foelker et al. 2016a; Long et al. 2009). Studies in South Africa found that the wood at the bases of pines was moister than that higher within the trunks, and *D. siricidicola* densities were also greater at the bases of trees; numerous studies have suggested that wood moisture content can influence activity of both *D. siricidicola* and *A. areolatum* (see Hurley et al. 2008). If the nematodes are less abundant higher in trees due to such an environmental variable, then direct competition with *I. l. ensiger* would be reduced. Alternatively, nematode mortality due to competition with the parasitoid could be masked by very strong host density dependence by the nematodes.

The native community of parasitoids that were present in the northeastern US before invasion by *S. noctilio* readily use *S. noctilio* as a host. On average, 37% of the *Sirex* from a tree was parasitized, ranging from 0 to 100%. This overall parasitism is similar to what was found by Krivak-Tetley et al. (2022) in a smaller study in this region, and by Haavik et al. (2015) using experimentally-exposed logs. We found the frequency of parasitism by *I. l. ensiger* increased with host density, and the frequency of parasitism by rhyssines decreased with increasing host density, leading to no association of overall parasitism with host density (Table 3). Different parasitoid species often respond differently to host density. Some species respond to high host density by aggregating, which leads to a positive dependent rate of parasitism (Walde and Murdoch 1988; Ives 1992). Indeed, *I. l. ensiger* has been shown to be attracted to the fungus associated with *S. noctilio* (Martinez et al. 2006; Faal et al. 2021) and to increase residence time on trees at increased *S. noctilio* density (Corley et al. 2010). However, in this complicated system, Foelker et al. (2016a) found no association of rate of parasitism by *I. l. ensiger* with host density while Krivak-Tetley et al. (2022) found a host density association for *I. l. ensiger* in *Pinus resinosa*, the pine predominantly sampled in this study, but not in *Pinus sylvestris*. Such differences between studies are not surprising where there is density dependence, especially when studies are conducted at different host densities. Our study was conducted over a wide range of host densities.

The rhyssine species showed higher parasitism at low host density. If parasitoids do not respond to host density the fraction parasitized can appear higher at very low host density than at high host density, simply reflecting the population size of foraging females (Walde and Murdoch 1988). This same pattern could also be due to competi-

tion between the rhyssines and *I. l. ensiger*. The latter species parasitizes *Sirex* eggs or young larvae (Foelker and Parry 2021) which makes it likely to be the superior competitor, since later-arriving endoparasitoids rarely are able to kill the parasitoid already developing in a host (van Nouhuys and Punju 2010; Cusumano et al. 2016). We only found a significant negative association between the parasitoid wasps at low host densities, where the fraction of hosts parasitized by rhyssines was highest. At higher host densities the frequency of parasitism by rhyssines was low, so the chance of both species parasitizing the same host individuals was unlikely, especially if there is some spatial segregation of parasitoid species within trees (Long et al. 2009; Foelker et al. 2016a).

As a caveat, the interactions between parasitoids and *S. noctilio* is complicated to evaluate due to variable voltinism of both rhyssines and *S. noctilio* (Foelker et al. 2016a). In particular, rhyssines have been thought to oviposit on late instar siricids in spring but then only emerge the following spring (Foelker and Parry 2021). However, it has also been suggested that two generations of rhyssines could possibly occur per year (Foelker and Parry 2021), which is supported by findings in this study, in which rhyssines emerged from the same wood in the same year as *S. noctilio*. In addition, there is the complication that *S. noctilio* has been found to oviposit in the same trees over multiple years (Haavik et al. 2018) and, once developing within a tree, some of the *S. noctilio* require more than one year for development (Ryan et al. 2012; Myers et al. 2014; Hajek et al. 2017).

In this study the native woodwasp, *S. nigricornis* occurred at much lower densities than *S. noctilio*, with the majority emerging early in the study, between 2011 and 2014 (Suppl. material 1); this supports the hypothesis that *S. noctilio* is the more successful competitor (Hajek et al. 2017). Of the 26 trees from which *S. nigricornis* emerged, *S. noctilio* also emerged from 88.5% of them. The local high densities of *S. noctilio* can impact the native woodwasp *S. nigricornis* in several ways. The large populations of *S. noctilio* could directly compete with *S. nigricornis* for trees in which to oviposit, especially because *S. nigricornis* is considered a less aggressive colonizer (i.e., needing weaker trees than *S. noctilio*) and most oviposit after *S. noctilio* (Hartshorn 2021). Secondly, when both woodwasps occupy the same tree, which creates higher woodwasp densities, parasitism by the nematode and *I. l. ensiger*, which are positively host density dependent, would be higher than if *S. nigricornis* occurred alone (van Nouhuys and Kraft 2012). Finally, high *S. noctilio* population densities can drive up the shared parasitoid and nematode populations in a forest, which could cause *S. nigricornis* to decline, an example of spillback by an invasive species (Kelly et al. 2009). Such apparent competition, driven by shared natural enemies, can have a strong impact on insect communities (van Nouhuys and Hanski 2000; Holt and Bonsall 2017).

In summary, this study of invasive *S. noctilio* and its introduced and native natural enemies emerging from 204 naturally infested trees over eight years, allowed for a robust analysis of the distribution of *S. noctilio* among trees, and for an exploration of the complex association of host and natural enemies over a large range of natural host densities. We found a strong pattern of aggregation by the woodwasp in a subset of the trees it occupied. Parasitism by the nematode *D. siricidicola* increased with host

density, making its distribution also aggregated. Parasitism by the native woodwasp parasitoid *I. l. ensiger* was high and also increased with host density, suggesting that this wasp may contribute to the control of the woodwasp. Additionally, though both the nematode and *I. l. ensiger* were positively host density dependent, there was little evidence of direct competition between the parasitoid and the nematode. The suite of native rhyssine parasitoids of *Sirex* were less abundant and occurred mostly where host densities were low. While our study indicates that they suffer from competition with *I. l. ensiger*, their population level relationship with the host and the other parasitoids may be complicated by a variation of voltinism.

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Supplementary material 1

The number of *Sirex*, nematodes, and parasitoids collected from each site, each year.

Authors: Saskya van Nouhuys, David C. Harris, Ann E. Hajek

Data type: Occurance

Explanation note: Data table showing the number of individuals of each species collected as part of this study.

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